



Bridgewater State University

## Virtual Commons - Bridgewater State University

---

Honors Program Theses and Projects

Undergraduate Honors Program

---

12-14-2018

### Using Clay Models to Measure Seasonal Predation on Eastern Red-Backed Salamanders

Emma Perry  
*Bridgewater State University*

Follow this and additional works at: [https://vc.bridgew.edu/honors\\_proj](https://vc.bridgew.edu/honors_proj)



Part of the [Biology Commons](#)

---

#### Recommended Citation

Perry, Emma. (2018). Using Clay Models to Measure Seasonal Predation on Eastern Red-Backed Salamanders. In *BSU Honors Program Theses and Projects*. Item 425. Available at: [https://vc.bridgew.edu/honors\\_proj/425](https://vc.bridgew.edu/honors_proj/425)  
Copyright © 2018 Emma Perry

This item is available as part of Virtual Commons, the open-access institutional repository of Bridgewater State University, Bridgewater, Massachusetts.

Using Clay Models to Measure Seasonal Predation on Eastern Red-Backed Salamanders

Emma Perry

Submitted in Partial Completion of the Requirements for  
Departmental Honors in Biology

Bridgewater State University

December 14, 2018

Dr. M. Caitlin Fisher-Reid, Thesis Advisor  
Dr. Kenneth Adams, Committee Member  
Dr. Kevin Curry, Committee Member

## Table of Contents

<b>Abstract</b>	<b>3</b>
<b>Introduction</b>	<b>4</b>
<b>Methods</b>	<b>10</b>
<b>Results</b>	<b>12</b>
<b>Discussion</b>	<b>15</b>
<b>Acknowledgements</b>	<b>19</b>
<b>References</b>	<b>20</b>

**Abstract**

One of the many gaps we have in our knowledge of salamanders is that of predation. Most studies suggest that salamanders are eaten mainly by birds and snakes, but there are still several unanswered questions: What other types of animals tend to prey on salamanders? Is there any difference in predator type during different times of the year? In order to answer these questions, I studied predation on one particular species of salamander, *Plethodon cinereus* (eastern red-backed salamander). Models of the two primary color morphs of *P. cinereus* (striped and unstriped) were created using impressionable clay to determine types and patterns of predation based on bite marks left in the clay. Models were deployed for two-week periods during multiple seasons (Fall 2017, Spring 2018, Fall 2018) and checked daily for signs of predation. Results revealed a variety of potential predator marks, including those left by rodents, slugs, birds, and some of which were unidentifiable, or models went missing. Unfortunately, there were few bird markings, and the slug and rodent markings are likely to be curiosity-driven taste-testing and not reflective of actual predation on salamanders. Overall, there was a significantly higher rate of predation in Fall 2017 compared to that in Spring 2018 and Fall 2018, suggesting acclimation to model presence. There was also a marginally significant difference in type of predator markings found, rodent being dominant, but no significant difference between predation on striped versus unstriped, across all seasons. Although the technique of clay modeling has been shown to be a useful method for measuring predation on various small terrestrial species, and only recently for *P. cinereus*, my experience in this study was not as successful. More than one flaw was discovered in this system, and thus, the validity and possibility for improvement is also discussed, with plans for continuation of the study in Spring 2019.

## Introduction

Researchers have long recognized the important role that terrestrial salamanders have in forest ecosystems (e.g., Petranka 1998, Davic and Welsh 2004). By using terrestrial salamanders as a focal organism to study the changes in geographic range, population dynamics, and interactions with other species, we might be able to better understand and evaluate certain changes in many other organisms, as well as the communities and ecosystems these organisms find themselves in. Terrestrial salamanders in the family Plethodontidae are arguably one of the most important animals in a forest ecosystem due to the wide variety of niches they occupy, their special physiology, and their abundance (Pough et al. 1987). Terrestrial salamanders are fundamental to their ecosystem as both predators and prey: they help regulate invertebrate species diversity and population sizes by consuming many of the smaller forest floor organisms (Davic and Welsh 2004, Sullivan et al. 2003). Salamanders then convert the food they consume into biomass, which provides high-quality energy and nutrients to the larger animals that prey on salamanders (Davic and Welsh 2004, Sullivan et al. 2003). In terms of their physiology, salamanders in the family Plethodontidae (which is the largest family of salamanders, accounting for about two-thirds of known salamander species; Amphibiaweb 2018) are lungless ectotherms that breathe entirely through their skin, so their survivability is greatly dependent on specific temperature and moisture tolerances (Petranka 1998; Milanovich et al. 2010). They are limited to relatively cool and wet microhabitats, and tend to remain in caves, underground, beneath rocks, logs and leaf litter, or in freshwater streams. Therefore, plethodontids are especially sensitive to changes in climate, and global climate change is expected to have a stronger impact on them compared to other forest animals (Pough et al. 1987). In addition, plethodontid salamanders are the most abundant predatory vertebrate species in northeastern United States forests (Davic and

Welsh 2004; Milanovich et al. 2010). Their population sizes and geographic ranges seem to remain relatively stable, making them an excellent indicator organism when attempting to understand current and prospective future changes in forest ecosystems (Davic and Welsh 2004; Milanovich et al. 2010). All of these characteristics of plethodontid salamanders have led to their increased use in studies on population dynamics within forest ecosystems.

Terrestrial plethodontids are small, nocturnal salamanders that spend much of their time hiding under various substrates. Yet, in spite of spending much of their time hidden, they are known to practice a range of techniques for avoiding predation while they themselves are foraging, including chemical cues, tail autotomy, toxic skin secretions, mimicry, and anti-predator postures (Pough et al. 1987, Davic and Welsh 2004). Salamanders are thought to be prey for a variety of animals, including birds, small mammals, snakes, fish, insects, frogs, and even other salamanders (Davic and Welsh 2004). The two most well-studied and well-documented predators of terrestrial salamanders are birds and snakes (Brandon and Huheey 1975, Howard and Brodie 1973, Brodie and Brodie 1980). There are a tremendous number of bird species on earth, so it would be difficult to determine whether each species finds plethodontids palatable. However, some studies suggest there are a few particular bird species which regularly eat terrestrial salamanders, including robins, domestic chickens, blue jays, and brown thrashers (Brandon and Huheey 1975, Howard and Brodie 1973, Brodie and Brodie 1980). When predating on terrestrial salamanders, birds tend to peck at them for several minutes all over their bodies, and then viciously wave the salamanders in the air and smack them against nearby substrates until the salamanders are motionless, after which they are swallowed whole (Brandon and Huheey 1975, Labanick 1984). In these studies, birds were often found to fall victim to the anti-predator behaviors of the salamanders, specifically tail autotomy and

aposematism (and aposematic mimics; Labanick 1984, Brodie and Brodie 1980). Tail autotomy occurs when a salamander detaches and drops the end of its tail to distract predators long enough to escape being eaten. Aposematism is the use of bright coloration to warn of toxic or otherwise dangerous traits (Labanick 1984).

Comparatively, snakes are not easily fooled by tail autotomy or aposematism, but rather have trouble maintaining control of captured salamanders that release sticky or toxic secretions or adopt anti-predator postures making them difficult to swallow. In studies conducted on snake predation, garter snakes are often used as the sole predator, mostly due to their abundance in most salamander habitats (Ducey et al. 1993). When predating on terrestrial salamanders, snakes initially bite at the rear end of the salamander, usually hitting the tail (resulting in autotomy and consumption of the tail) or just in front of or just behind the hind legs (Venesky and Anthony 2007). If the latter occurs, the salamander reacts with wild posturing and erratic movements or with the release of sticky or toxic secretions, in an effort to escape from the snake's mouth (Arnold 1982). Whether or not the salamander successfully escapes in any case depends on its performance in anti-predator behaviors, predator efficiency, and inevitably, the situational environment and surroundings.

Recently, there have been noticeable declines in salamander populations (Davic and Welsh 2004). There have been a variety of hypotheses regarding the causes of this decline, including increased predation or anthropogenic effects, such as chemical pollution and habitat loss, along with global climate change and infectious diseases (Collins and Storfer 2003). Climate change in itself has been shown to cause shifts in species abundances, migrations, and interactions, with impacts becoming more prominent in ecosystem food chains. Rapid changes resulting in new temperature and precipitation patterns can cause species to move to different

locations, or worse, cause declines in abundance, which subsequently lead to extinction, due to an inability to tolerate the new climate conditions. These changes may directly or indirectly affect one or more species, positively or negatively, but with no doubt causing a cascade of events involving decreased biodiversity due to inability to adapt (see review in Cahill et al. 2013). For example, if a change in climate was to prompt an increase in one species of bird that predated on a species of salamander, then there might be an expected decrease in the salamander population. However, in order to determine how climate change may drive population declines of salamanders, the gaps in the knowledge we currently have on salamanders must be identified. One of the many poorly-studied areas seems to be that of predation, as there are several unanswered questions pertaining to the predation of terrestrial salamanders: What types of animals tend to prey on salamanders? Are there seasonal changes in predator type that may be exacerbated in future climates?

Several studies have used a specific technique for measuring predation on amphibians and reptiles, in which clay models of the prey species are made and placed in the environment to observe patterns in predation based on model coloration, placement, and predator type (e.g., Pfennig et al. 2007; Saporito et al. 2007; Fitzpatrick et al. 2009; Grant et al. 2018). The soft clay of the model keeps a record of each predation attempt as a mark in the clay. Studies by Fitzpatrick et al. (2009) and Grant et al. (2018) specifically focus on salamanders and outline the processes of shaping and deploying clay salamander models to discover predation types and patterns. Model designs were only slightly different in coloration between these two studies, but both studies are based on the assumption that the predators are primarily visual hunters. In order to improve sample sizes of predation attempts, Grant et al. (2018) placed models on white paper to make them more obvious to predators and Fitzpatrick et al. (2009) added a food reward to the



underside of the models.

In this study, I will be focusing on a particular species of plethodontid salamander, the eastern red-backed salamander (*Plethodon cinereus*). This species is commonly found throughout forests in northeastern North America, and is highly abundant (Burton and Likens 1975). *Plethodon cinereus* is known for its color polymorphism, with two primary color morphs: striped, having a red pigmented stripe down the length of the dorsal side, and unstriped, lacking the red stripe and having a completely black coloration (Fig. 1; Petranka 1998). Several studies have observed a correlation between warmer climates with higher unstriped morph abundance (e.g., Lotter and Scott 1977; Anthony et al. 2008), suggesting that the morphs will respond to climate change differently, however these patterns are inconsistent across the range of *P. cinereus* and the genus, which contains 7 other polymorphic species (see review in Fisher-Reid and Wiens 2015). To my knowledge, no one has looked at how species interactions, in particular predation, might change with climate change.



**Figure 1:** The two most common color morphs of *P. cinereus*, unstriped in the upper left and striped in the lower right. Photo used with permission from M.C. Fisher-Reid.

Therefore, I will be exploring some of the unanswered questions focused around terrestrial salamander predation using clay models of salamanders to record predation attempts across different seasons. In particular, I am interested in if primary predator type (e.g., bird,

small mammal) varies with season and if visual predators prefer one color morph over another. I hypothesize that predation attempts in Bridgewater, MA will reflect that birds and small mammals are the primary predators of salamanders. This hypothesis does not include snakes and other amphibians, because they often rely on chemosensory capabilities when hunting for prey and this study is focusing on visual predation. Previous research in Bridgewater State University's (BSU) forest suggest that salamanders have increased surface activity in the fall compared to spring (M.C. Fisher-Reid, unpublished data). Therefore, I predict that more predation attempts will occur during the fall compared to spring. Lastly, I predict that there will be higher predation rates on striped morphs than on unstriped morphs, because striped morphs are more obviously visible on the forest floor, due to their red stripe.

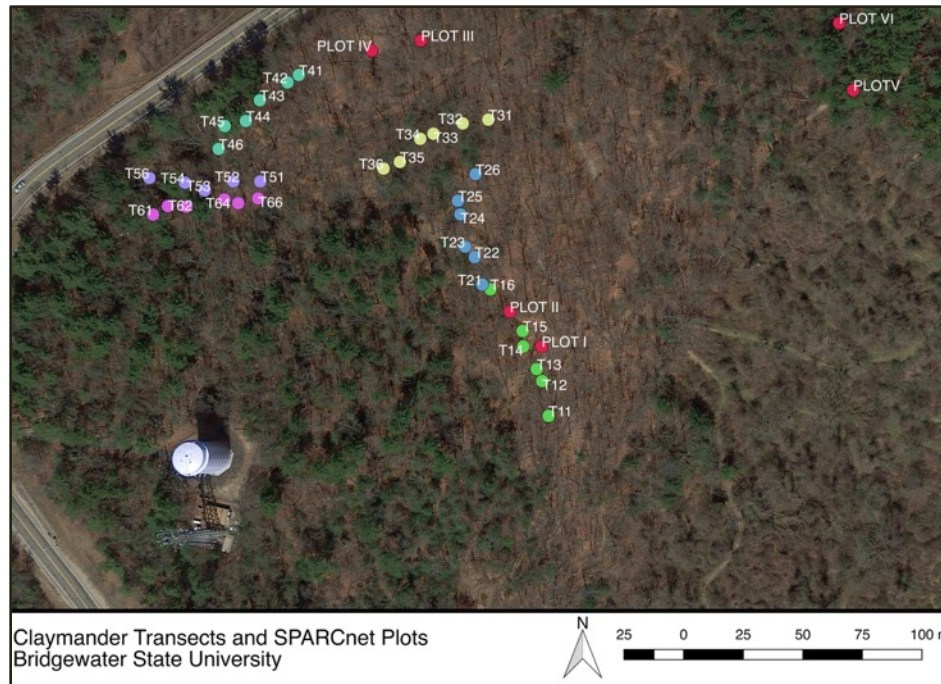
## Methods

I tested for the types of predators and seasonal patterns of predation of *P. cinereus* by creating and deploying impressionable clay salamanders in the Great Hill Forest on the BSU campus. I compared the predation markings left in the clay during three sampling periods covering two seasons: Fall and Spring (October 2017, May 2018, and October 2018) for both color morphs. Using gray and red impressionable clay, I made 400 *P. cinereus* salamander models, 200 of each color morph. Each model has a trunk with a defined head, tail, and four thin limbs, along with a bent aluminum wire on the ventral side to anchor the model to the ground, measuring about 10 cm in length (Fig. 2). These models are similar in style to those used in other salamander predation studies (e.g., Fitzpatrick et al. 2009; Grant et al. 2018; but particularly Grant et al. 2018).



**Figure 2:** "Before" pictures of striped (left) and unstriped (right) clay models in the forest.

I deployed the models across six, non-overlapping 50 m transects, with at least 10 m between transects (Fig. 3). Each transect contained six clay models of alternating color morphs, for a total of 36 deployed models and 18 models per morph. The starting morph for each transect was randomly determined using a coin flip. For each sampling period, I placed trail cameras on trees at three of the six transects, in hopes of catching visuals of potential predators in the area.



**Figure 3:** Map of clay salamander transect locations within Great Hills Forest at BSU. The circles represent model placement on each of six transects (transects represented by different colors). The red circles with plot labels are active salamander research plots for another project. Image made in QGIS v. 2.18 and used with permission from M.C. Fisher-Reid

During each season, I deployed salamander models for two weeks. During each deployment period, I checked all 36 models daily for predation marks left in the clay by forest animals that attempt to eat the models. In order to keep a record of predation, a “before” picture is taken of each model when first deployed. If marked by a predator, an “after” picture is taken and the model is removed and replaced with a new, unmarked model, which was also photographed upon deployment. After the two-week period, all of the models were removed from the forest and flags marking model locations were left to ensure model placement remains constant in all seasons. Data from all three sampling seasons were compared and analyzed using Binomial and Fisher’s Exact Tests.

## Results

At the end of the first two-week deployment in Fall 2017, a total of 31 salamander models were recovered with predation marks split nearly evenly between striped and unstriped morphs (Table 1). Based on pictures of the predation markings left in the clay, some of the possible predators may include rodents and slugs (Fig. 4). However, there were many markings that were unidentifiable as any one particular animal (Table 1). The rodent markings often showed clear bites consisting of top and bottom incisors, and the slug markings showed trails of squiggly patterns in all directions (Fig. 4). During Fall 2017, there were no obvious marks suspected of bird predation (Table 1).



**Figure 4:** “After” pictures of striped with rodent marking (left) and unstriped with slug marking (right).

During successive sampling seasons, Spring 2018 and Fall 2018, I observed much fewer model-predator interactions, with a total of eight salamander predation attempts recovered during each season (Table 1). Again, these attempts were nearly evenly split between striped and unstriped morphs during both seasons. Based on pictures of the predation markings left in the clay, possible predators during these two seasons were similar to those found in the Fall 2017 sampling, including rodents, birds, and slugs, and some were still unidentifiable. Fewer slug



markings were observed, overall, with the most common predator being rodent in both Spring 2018 and Fall 2018.

**Table 1:** Predation data by season, morph, and predator type. (\*one of the unknown marks was a missing model)

<b>Season &amp; Morph</b>	<b>Rodent</b>	<b>Slug</b>	<b>Bird</b>	<b>Unknown</b>	<b>Total</b>
<i>Fall 2017</i>	<i>12</i>	<i>8</i>	<i>0</i>	<i>11</i>	<i>31</i>
Striped	5	5	0	5	15
Unstriped	7	3	0	6	16
<i>Spring 2018</i>	<i>0</i>	<i>2</i>	<i>1</i>	<i>5</i>	<i>8</i>
Striped	0	2	0	3	5
Unstriped	0	0	1	2	3
<i>Fall 2018</i>	<i>5</i>	<i>0</i>	<i>1</i>	<i>2*</i>	<i>8</i>
Striped	2	0	1	1	4
Unstriped	3	0	0	1	4

I tested several hypotheses regarding seasonal and morph-specific predation. These tests revealed no significant difference in predation on striped versus unstriped models ( $P = 0.91$ , Fisher's Exact Test) and a marginally significant difference in the types of identified predators based on markings in the clay models when all three seasons were compared ( $P = 0.06$ , Fisher's Exact Test). Both rodents and slugs were more common in Fall than Spring. This pattern is likely due to the much higher sample sizes of Fall 2017 compared to the other two seasons.

Analysis of Fall 2017 against Spring 2018 results showed no significant morph-specific predation ( $P = 0.38$ , Fisher's Exact Test), but there was a significant difference in the dominant type of predator between the two seasons. Rodents and slugs were significantly more common predators in Fall compared to Spring, ( $P = 0.025$ , Fisher's exact). There was also a significant decrease in overall predation attempts from Fall 2017 ( $N = 31$ ) to Spring 2018 ( $N = 8$ ;  $P = 0.001$ , Binomial Test; Fig. 5).

Analysis of Spring 2018 against Fall 2018 results showed no significant morph-specific predation ( $P = 0.50$ , Fisher's Exact Test), but there was a marginally significant difference in types of predators recorded during the two seasons ( $P = 0.048$ , Fisher's Exact Test). Rodent predation was more common during Fall compared to Spring. There was no significant difference in total predation counts for Spring 2018 versus Fall 2018 ( $P = 0.60$ , Binomial Test; Fig. 5).

Analysis of Fall 2017 against Fall 2018 results showed no significant morph-specific predation ( $P = 0.62$ , Fisher's Exact Test). There was a marginally significant difference in the types of predators, with slugs more common in Fall 2017 compared to Fall 2018 ( $P = 0.037$ , Fisher's Exact Test). Similar to the first dual-comparison, total predation counts in Fall 2017 versus Fall 2018 was significantly different, showing a steep decrease in predation attempts from Fall 2018 to Fall 2017 ( $P = 0.003$ , Binomial Test; Fig. 5).

During all three seasons, the trail cameras recorded deer, people, and several small mammals, including foxes, raccoons, and squirrels (Fig. 6). Interestingly, no birds were recorded on the trail cameras. Rodents (i.e., squirrels) were also rarely captured compared to other medium and large mammals.

## Discussion

In this study, I used clay models to test patterns of visual predation on the terrestrial salamander species *P. cinereus* over two different seasons in which they are active. I predicted that expected predators would be primarily birds and small mammals that typically eat salamanders, that higher predation rates would occur on the striped model over the unstriped model, and that higher predation rates would occur in the fall season over the spring season. Data from the three sampling seasons, including two falls and one spring, have shown largely negative results regarding these predictions. Although a handful of bird markings were left in the models (Table 1), the primary predator found across the seasons was rodents, which are generally nocturnal, and thus not likely to be distinguishing between color morphs of salamanders. Overall there was no difference in predation on striped versus unstriped models, either in individual or across seasons. This again suggests limited visual predation attempts, as other studies have observed frequency-dependent predation by color (Fitzpatrick et al. 2009). Initially, there appeared to be a strong bias toward fall predation, as predicted (Fall 2017 is significantly greater than Spring 2017; Fig. 5). However, with Fall 2018 data, this pattern disappears, as Spring 2018 and Fall 2018 show identical levels of predation (Fig. 5). Across all three seasons, there is an overall decrease in predation attempts, with Fall 2017 having double the number of predation markings found in Spring 2018 and Fall 2018 combined (Fig. 5). This is likely due to predator acclimation to model presence in the forest. In other words, the greater predation attempts observed in Fall 2017 might have been predators taste-testing the models, and when the models returned for the subsequent sampling periods, the majority of predators already knew what they were and let them be. Additionally, a newly established den of red foxes (*Vulpes vulpes*) was discovered across a campus road from three of the transects (4, 5, and 6) in Spring 2018, and this



may partly explain the decline in predation markings, particularly those by rodents as populations might have declined with the presence of a new predator.

For several decades, *P. cinereus* has been a model organism in various ecological studies, however, only recently has clay modeling of the species become prominent as a tool for measuring predation. One of the underlying goals of this study was to test the validity of this clay model technique without bait (Fitzpatrick et al. 2009) or contrasting backgrounds (Grant et al. 2018). Most of the predation discovered through this study seemed to be from accidental predators, as both slugs and rodents tend to be herbivorous. The nocturnal habits of rodents suggest their markings were most likely curiosity-based, and the slugs might have simply found something in the clay palatable (e.g., calcium content). I expected much more bird predation than I observed, and given my results, bird predation might not be solely visual, as was being tested. If bird-specific predation is to be examined further, techniques similar to those used in the studies by Fitzpatrick et al. (2009) and Grant et al. (2018) might be considered to make the models more obvious and attractive to bird predators, which do not seem to hunt using purely visual recognition. However, these adjustments may have the drawback of being unrealistic, and not reflect how birds and salamanders truly interact in nature.

After completion of multiple seasons using the clay model technique, I have determined some experimental flaws that should be adjusted to possibly improve the outcomes of this type of study. For example, in this study models were only checked once per day, in the middle of the day, so as to avoid high predator feeding times and scaring off any potential predators. The purpose of the trail cameras was, therefore, to catch any predators that might be present throughout the rest of the 24-hour period. However, ideally a small, inconspicuous camera should be on each individual model to observe everything that comes into contact.

Unfortunately, this would be prohibitively expensive and difficult to set up and secure in a high-use forest on a college campus, like the one in which this study was conducted. Additionally, there are a few underlying questions regarding the validity of this technique: How do we know if the predation markings left in the clay reflects actual predation patterns in natural settings, as opposed to animals merely curious about an unknown object found on the forest floor? Might some of the markings left in the clay be false positives, particularly when the clay might be extra soft or hard based on external temperatures? One possible means of answering these questions might be to add a control factor, for example a randomly shaped ball of clay placed in the forest, in order to normalize the biting patterns. Another feasible adjustment to this study might be in model design; the models used in this study were made separately by rolling and molding the clay by hand, and therefore were all slightly different. This might be acceptable, seeing as no two live salamanders are the same, though this also adds more inconsistency, so changing this to be more realistic and uniform would again act as a control. Furthermore, a more realistic model designed using a mold (e.g., as in Fitzpatrick et al. 2009), may elicit greater responses from predators.

With the recent decline in amphibian species, scientists are exploring new tactics to discover how species interactions like predation may contribute to the decline. Studies published in the past decade have attempted to understand the predation on certain terrestrial species by using impressionable clay to make individual models and observe bite mark patterns left by predators. Thus far, this technique seems to have some promise going forward, however there are clearly flaws that need to be addressed. That being said, this could possibly be a highly effective method of measuring predation on many terrestrial amphibian species if improved. Terrestrial

salamanders play an important role in forest ecosystems, and increasing knowledge on the many species should continue to be a focus in ecological research.

## **Acknowledgements**

This project was funded by the Office of Undergraduate Research at Bridgewater State University through two Adrian Tinsley Program (ATP) semester grants awarded to Emma Perry for Fall 2017 and Spring 2018. A tremendous thank you to Dr. M. Caitlin Fisher-Reid, who served as both director and mentor on this project, and worked just as hard to complete it. The author would also like to thank: Elena Babicz, Sarah Couto, Mariah Fossella, Alex O’Roak, Matthew Tucker, and Julia Whalen. for their help with making clay salamanders and setting up transects in the field; and the Great Hill forest trail manager Dan Rezendes for his assistance during model monitoring for two weeks in “his” forest. Thank you to Dr. Christopher Bloch for statistical advice. Thank you to Dr. Ken Adams for being on my thesis committee, along with all of the support and encouragement throughout the process. Thank you to Dr. Kevin Curry for being on my thesis committee and contributing greatly to the conversation and details on the subject area. Lastly, thank you to all who have taken the time to provide support, encouragement, and kindness that empowered me to finish strong.

## References

- AmphibiaWeb: Information on amphibian biology and conservation [web application]. 2018. Berkeley, California: AmphibiaWeb. Available at <http://www.amphibiaweb.org>. Accessed September 17, 2018.
- Anthony, C.D., M.D. Venesky, and C.A.M. Hickerson. 2008. Ecological separation in a polymorphic terrestrial salamander. *Journal of Animal Ecology* 77: 646-653.
- Arnold, S. 1982. A Quantitative Approach to Antipredator Performance: Salamander defense against snake attack. *Copeia* 1982: 247-253.
- Brandon, R. and J. Huheey. 1975. Diurnal activity, avian predation, and the question of warning coloration and cryptic coloration in salamanders. *Herpetologica* 31: 252-255.
- Brodie Jr, E.D. and E.D. Brodie III. 1980. Differential avoidance of mimetic salamanders by free-ranging birds. *Science* 208: 181-182.
- Burton, T.M. and G.E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook experimental forest, New Hampshire. *Copeia*: 541-546.
- Cahill, A.E., M.E. Aiello-Lammens, M.C. Fisher-Reid, X. Hua, C.J. Karanewsky, H.Y. Ryu, G.C. Sbeglia, F. Spagnolo, J.B. Waldron, O. Warsi, and J.J. Wiens. 2013. How does climate change cause extinction? *Proc. R. Soc. B*, 280: 1-9.
- Collins, J.P. and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. *Diversity and Distributions* 9: 89-98.
- Davic, R.D. and H.H. Welsh Jr. 2004. On the ecological roles of salamanders. *Annual Review of Ecology, Evolution, and Systematics* 35: 405-434.
- Ducey, P., E. Brodie, and E. Baness. 1993. Salamander tail autotomy and snake predation:

- Role of antipredator behavior and toxicity for three neotropical *Bolitoglossa* (Caudata: Plethodontidae). *Biotropica* 25: 344-349.
- Fisher-Reid, M.C. and J.J. Wiens. 2015. Is geographic variation within species related to macroevolutionary patterns between species?. *Journal of Evolutionary Biology* 28: 1502-1515.
- Fitzpatrick, B.M., K. Shook, and R. Izally. 2009. Frequency-dependent selection by wild birds promotes polymorphism in model salamanders. *BMC ecology* 9: 1-6.
- Grant, A.H., T.S. Ransom, and E.B. Liebgold. 2018. Differential survival and the effects of predation on a color polymorphic species, the red-backed salamander (*Plethodon cinereus*). *Journal of Herpetology* 52: 127-135.
- Howard, R., and E. Brodie. 1973. A Batesian mimetic complex in salamanders: Responses of avian predators. *Herpetologica* 29: 33-41.
- Labanick, G. 1984. Anti-predator effectiveness of autotomized tails of the salamander *Desmognathus ochrophaeus*. *Herpetologica* 40: 110-118.
- Lotter, F. and N.J. Scott Jr. 1977. Correlation between climate and distribution of the color morphs of the salamander *Plethodon cinereus*. *Copeia*: 681-690.
- Milanovich, J.R., W.E. Peterman, N.P. Nibbelink, and J.C. Maerz. 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. *PLoS One* 5: 1-10.
- Pfennig, D.W., G.R. Harper, A.F. Brumo, W.R. Harcombe, and K.S. Pfennig. 2007. Population differences in predation on Batesian mimics in allopatry with their model: selection against mimics is strongest when they are common. *Behavioral Ecology and Sociobiology* 61: 505-511.

- Pough, F.H., E.M. Smith, D.H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. *Forest Ecology and Management* 20: 1-9.
- Saporito, R.A., R. Zuercher, M. Roberts, K.G. Gerow, and M.A. Donnelly. 2007. Experimental evidence for aposematism in the dendrobatid poison frog *Oophaga pumilio*. *Copeia* 2007: 1006-1011.
- Sullivan, A.M., D.M. Madison, and J.R. Rohr. 2003. Behavioural responses by red-backed salamanders to conspecific and heterospecific cues. *Behaviour* 140: 553-564.
- Venesky, M.D. and C.D. Anthony. 2007. Antipredator adaptations and predator avoidance by two color morphs of the eastern red-backed salamander, *Plethodon cinereus*. *Herpetologica* 63: 450-458.